

A NEW DENDROCERATID SPONGE WITH RETICULATE SKELETON

MANUEL MALDONADO AND MARIA J. URIZ

Maldonado, M. & Uriz, M.J. 1999 06 30: A new dendroceratid sponge with reticulate skeleton. *Memoirs of the Queensland Museum* **44**: 353-359. Brisbane. ISSN 0079-8835.

A new encrusting dendroceratid sponge characterised by a skeletal network of ascending primary spongin fibers transversally interconnected by secondary fibers is described from the Alboran Sea (W Mediterranean). Primary fibers, provided with a subcircular basal plate for attachment to the substratum, are unbranched or poorly branched, fasciculate in most cases, with a pith containing foreign material, and a laminated bark. Secondary fibers are also laminated, usually lack any coring material, and may form fenestrated plates around the point where they anastomose to a primary fiber. The reticulation of the skeleton is loose and irregular, so that some primary fibers are interconnected through their basal portions only, some are interconnected along their apical portion, and some are even isolated, lacking any transversal interconnection. Although skeletal features of both the darwinellid genus *Aplysilla* and the dictyodendrillid genus *Igernella* are recognisable in this new sponge, it cannot be taxonomically assigned to either genus, unless the current diagnosis of one of them is modified. A reanalysis of the chemical, histological and skeletal evidence available to date gives little support to the hypothesis that reticulate skeletons appeared in Dendroceratida as a single evolutionary event. Consequently, we propose expanding the diagnosis of the genus *Pleraplysilla* to include species with an irregular network of secondary fibers, such as *Pleraplysilla reticulata* sp. nov. □ *Porifera*, *Keratose sponges*, *Dendroceratida*, *Pleraplysilla*, *Darwinellidae*, *Dictyodendrillidae*, *new species*.

Manuel Maldonado (e-mail: maldonado@ceab.esic.es) & Maria J. Uriz, Department of Aquatic Ecology, Centro de Estudios Avanzados de Blanes (CSIC), Camino de Santa Bàrbara s/n. Blanes 17300. Girona. Spain; 2 March 1999.

The siliceous skeleton that characterises most sponges in the class Demospongiae is replaced by a skeleton of spongin fibers in a group of sponges that comprises the orders Verongida, Dictyoceratida and Dendroceratida. To provide skeletal support to the bulk of soft sponge tissue, spongin fibers may be either anastomosed to form a network or organised as sets of diversely dendritic, unconnected structures. Dendritic skeletons occur in some Verongida and some Dendroceratida, whereas reticulate skeletons occur in all three orders.

Reticulate skeletons display a wide variety of models of organisation not only within orders, but also families. Differences involve morphology, orientation and dimensions of the basic mesh, as well as several degrees of diversification, both in size and structure, of the anastomosing fibers (e.g. Van Soest, 1978; Bergquist, 1980, 1995, 1996; Bergquist et al., 1998). Given such a structural diversity, the acquisition of a reticulate skeleton is likely to have evolved independently in Dictyoceratida, Verongida and Dendroceratida. This idea is implicitly assumed in the historical classification of these so-called 'fibrous' or 'keratose' sponges,

which are distributed in three different orders. Nevertheless, it is also assumed that the acquisition of a reticulate skeleton within the order Dendroceratida was a single, synapomorphic evolutionary step. Consequently, dendroceratid genera with reticulate and non-reticulate skeletons are placed in two different families (e.g. Bergquist, 1980, 1995, 1996; Bergquist et al., 1998): Dictyodendrillidae Bergquist (with a reticulate skeleton made of primary fibers interconnected by secondary fibers) and Darwinellidae Merejkowsky (with exclusively dendritic skeletons made of a single type of fiber). However, some chemical and histological studies have reported unexpected affinities between members of these two families. For example, studies on the diterpenoid chemistry (Bergquist et al., 1990) suggested a relationship between the dictyodendrillid genus *Igernella* Topsent (with a reticulate skeleton and spongin spicules) and darwinellid genera with a typically dendritic skeleton, such as *Darwinella* Müller (with spongin spicules) and *Pleraplysilla* Topsent (without spongin spicules). Similarly, studies on choanocyte chamber structure (Dendy, 1905; Vacelet et al., 1989; Boury-Esnault et al.,

1990) revealed that the genus *Dysidea* Johnston, traditionally included in Dictyoceratida, and members of the family Darwinellidae share a remarkable feature: the presence of eurypylous chambers. At first sight, these non-skeletal affinities do not appear to be consistent with the subdivision of Dendroceratida into Darwinellidae and Dictyopleraplysillidae on the basis of the skeletal pattern. Rather, chemical and histological affinities suggest that reticulate skeletons may have arisen independently in Dendroceratida more than once, so that families diagnosed on the basis of this skeletal trait would not represent monophyletic groups. Nevertheless, these non-skeletal features should not be considered as conclusive evidence for a new classification within Dendroceratida. Bergquist (1996) claimed that the reliability of chamber structure as a character to support a high level classification of keratose sponges is not great, since eurypylous chambers are not exclusively found in *Dysidea* and Darwinellidae, but they also occur in the verongid genus *Ianthella* Gray. Furthermore, although the available body of information from the diterpenoid chemistry and histology is clearly in conflict with a taxonomic scheme based on a separation between reticulate and dendritic dendroceratid genera, it fails to reveal any robust alternative pattern of taxonomic relationships. Thus, despite the fact that skeletal pattern remains the only exclusive familial characteristic supporting a division of Dendroceratida into Dictyodendrillidae and Darwinellidae (Bergquist, 1996), such a taxonomic scheme persists as the best option to date.

Here we describe a new dendroceratid sponge in which the skeletal traits of the Darwinellidae and the Dictyodendrillidae are combined, suggesting that even the skeletal criterion may not be as robust as first thought to maintain the current familial scheme in Dendroceratida. Unfortunately, the contribution of the new material described here to an understanding of the relationships in Dendroceratida has been undermined by two unfortunate mishaps. First, although several individuals of this new species occurred at the collection site, we only collected one specimen because we mistook them for material belonging to the common species *Darwinella muelleri* Schulze, which closely resembles the new species when under water. This would not be an insurmountable problem, if the collection site (the Alboran Island) had not been a remote Mediterranean location.

Unfortunately, the Alboran Island was only accessible via a costly scientific cruise. Second, the tissue of the holotype became somewhat macerated and therefore useless for providing information on choanocyte chamber structure, since, when we realised the importance of this specimen, it had already been exposed to air during dissection to obtain its skeletal fibers. In 1996, that is eight years after this collection, a second scientific cruise ('Fauna Ibérica - IV') visited the same collection site, but the team of divers failed to find any individuals from this new species. Ten years after its collection and despite the problems mentioned above, we have finally decided to record this material in the scientific literature for two reasons. First, the well-preserved skeletal traits of the specimen clearly indicate that it belongs to an undescribed species. Second, this material provides skeletal information that may be crucial in retracing the path of skeletal evolution in Dendroceratida as further information is gained.

MATERIALS AND METHODS

The material was collected by SCUBA from the sublittoral bottom of the Alboran Island (W Mediterranean: 35°56'45"N, 3°01'38"W; 24m deep) during the 'Ecopharm-I' Cruise in 1988. The specimen was fixed in a 4% formalin solution and stored in 70% alcohol. The skeletal arrangement was studied under dissecting and compound microscopes after partial dissection of the specimen. Its fibers were also studied under a Hitachi S-2300 SEM, after a process of dehydration in a graded series of ethanol, critical point and coating with gold palladium in an E-5000 sputtering.

The holotype is deposited in the collection of the Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain. For comparative purposes, we also examined several individuals of *Pleraplysilla spinifera* (Schulze) from the Alboran Island and the NE coast of Spain (authors' collection), the holotype of *Igernella mirabilis* Lévi from Indonesia (Zoölogisch Museum Amsterdam, ZMA: POR9316), Caribbean specimens of *Igernella notabilis* (Duchassaing & Michelotti) (authors' collection and ZMA POR6938 specimen), and a specimen of *Dendrilla cirsioides* Topsent from Banyuls (ZMA POR74).

SYSTEMATICS

Class **Demospongiae** Sollas
 Order **Dendroceratida** Minchin
 Familia **Darwinellidae** Merejkowsky

Pleraplysilla Topsent, 1905

Encrusting Darwinellidae with a fiber skeleton of ascending primary fibers that may be either isolated or diversely fused to each other with or without the development of secondary fibers. Primary fibers are short (few mm), simply or partially fasciculate, poorly branched or unbranched, with a laminated bark and a pith filled with debris, and stand on the substratum on which the sponge grows, attached by means of a small basal plate. Secondary fibers, when present, are concentrically laminated, without coring material or with scarce scattered inclusions. Spongin spicules are absent (emended).

Pleraplysilla reticulata sp. nov.

MATERIAL. HOLOTYPE: MNCN 1.01/182. W Mediterranean, Alboran Island, 35°56'45"N, 3°01'38"W; 24m depth.

ETYMOLOGY. Named for the reticulate condition of the fiber skeleton.

DESCRIPTION. Encrusting, 2x3cm, 0.5cm thick; dull yellow alive, with some lemon yellow zones; soft, slippery to touch, with some mucus on the surface; surface sparsely conulose; conules 1.5-2mm high and 2-4mm apart; oscules and ostia punctiform, grouped in depressed areas located among conules.

Choanosome fleshy, with tiny aquiferous channels; skeleton as a loose, irregular network made of ascending primary fibers transversally interconnected by secondary fibers (Fig. 1A-B); primary fibers non-branched or poorly branched, erect, attached to the substratum by means of a small basal plate (Fig. 2A, C). Fibers have a concentrically laminated bark and a pith containing foreign material (Fig. 1C). Two or more adjacent primary fibers usually fused, yielding fibers with fasciculate appearance (Fig. 1A-C); primary fibers <1cm long, 30-85µm wide, although they can reach 150µm in the fasciculate portions; basal plates 300-700µm in diameter; secondary fibers 20-40µm wide, concentrically laminated, usually lacking any coring material (Fig. 1D); fenestrated plates up to 300µm wide are formed around the point where a primary and

a secondary fiber contact (Figs 1B-C, 2B, D); spongin is almost colorless and highly transparent, especially in the secondary fibers and fenestrated plates.

The reticulation of the skeleton is quite irregular; some primary fibers are interconnected through their basal portions only, whereas others are interconnected along their apical portions, just under the ectosome; some primary fibers, especially those newly formed at the growing margins of the sponge, are even isolated, lacking any secondary interconnection; isolated fibers strongly resemble those of *Pleraplysilla spinifera*.

HABITAT. The specimen was found on the vertical side of a rocky block at 24m depth. Although only one specimen was collected for this study, at least six others were observed at the sampling site along with various specimens of the species *Clathrina clathrus* (Schmidt), *Aplysilla sulfurea* Schulze and *Pleraplysilla spinifera*.

REMARKS. To our knowledge, the species described in this study is the first dendroceratid sponge with reticulate skeleton recorded in the Mediterranean.

DISCUSSION

The skeletal features of this species suggest that it is closer to the genera *Pleraplysilla* and *Igernella* than to any other dendroceratid. Its primary fibers strongly resemble those of the genus *Pleraplysilla*, which also contain foreign material in the pith. Furthermore, anastomoses of adjacent primary fibers forming fasciculate primaries are not exclusive to this new species. Van Soest (1978) reported anastomoses of primary fibers to yield "vague meshes here and there" in the Caribbean species *Pleraplysilla stocki* Van Soest, 1978. However, the occurrence of a reticulate skeleton made of ascending primaries and interconnecting secondary fibers has not been reported in this genus to date. Such a trait does not coincide with the current diagnosis of either the genus *Pleraplysilla* or the family Darwinellidae (e.g. Bergquist, 1980). Rather, the network model suggests a relationship between the specimen collected and some dictyodendrillids, such as *Igernella* species that are characterised by an irregular reticulation made of ascending primaries transversally interconnected by secondary fibers (Van Soest, 1978; Uriz & Maldonado 1996). However, this new species does not match the current diagnosis of *Igernella*,

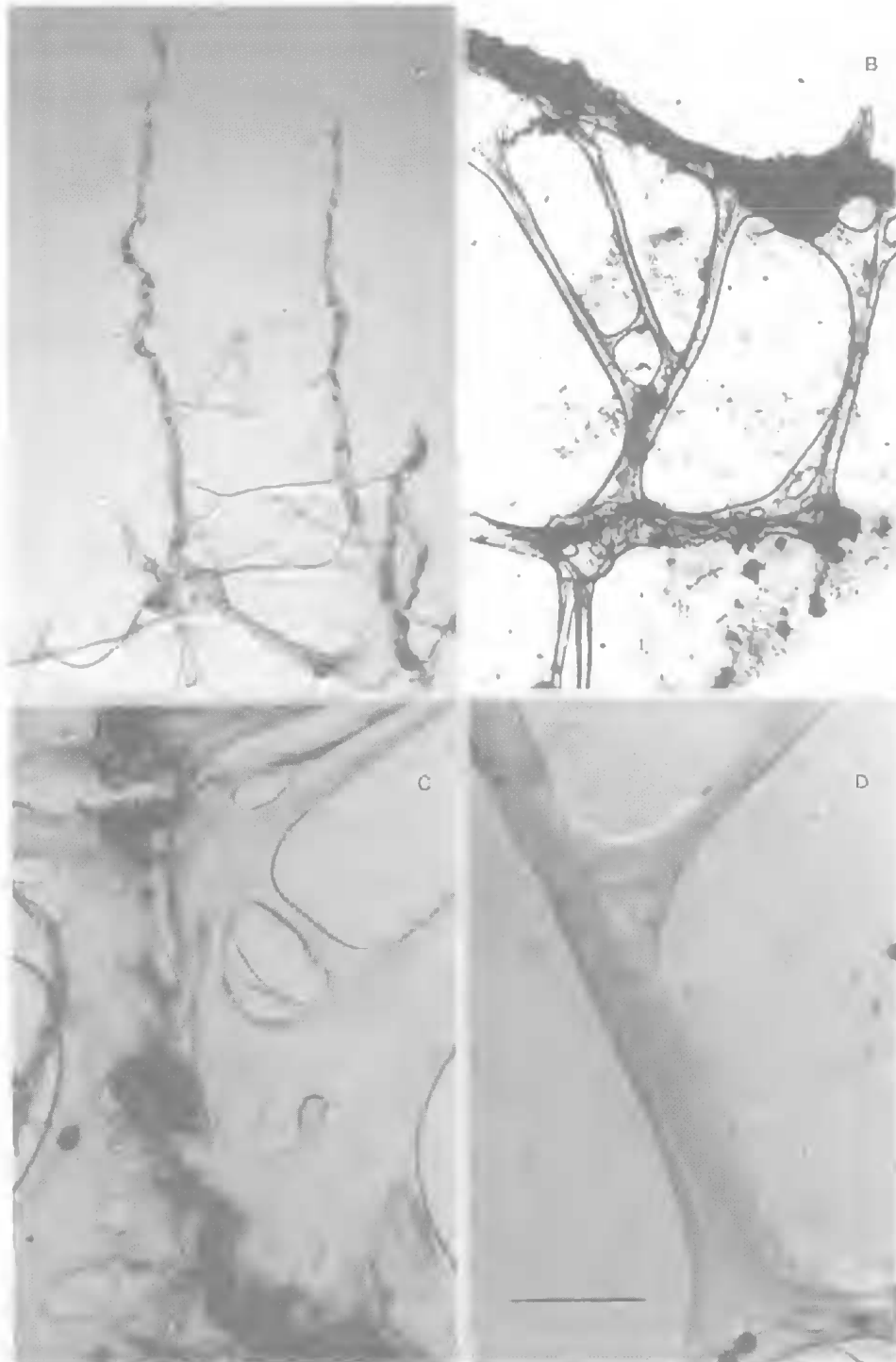


FIG. 1. *Aplysilla reticulata* sp. nov. A, General organisation of the skeleton. B, Detail of secondary reticulation interconnecting two cored primary fibers. C, Detail of a primary fiber showing a pith filled with debris. Fenestration can also be seen. D, Detail of the laminated structure of a secondary fiber. Scale bars A, 950 μ m; B, 420 μ m; C-D, 50 μ m.

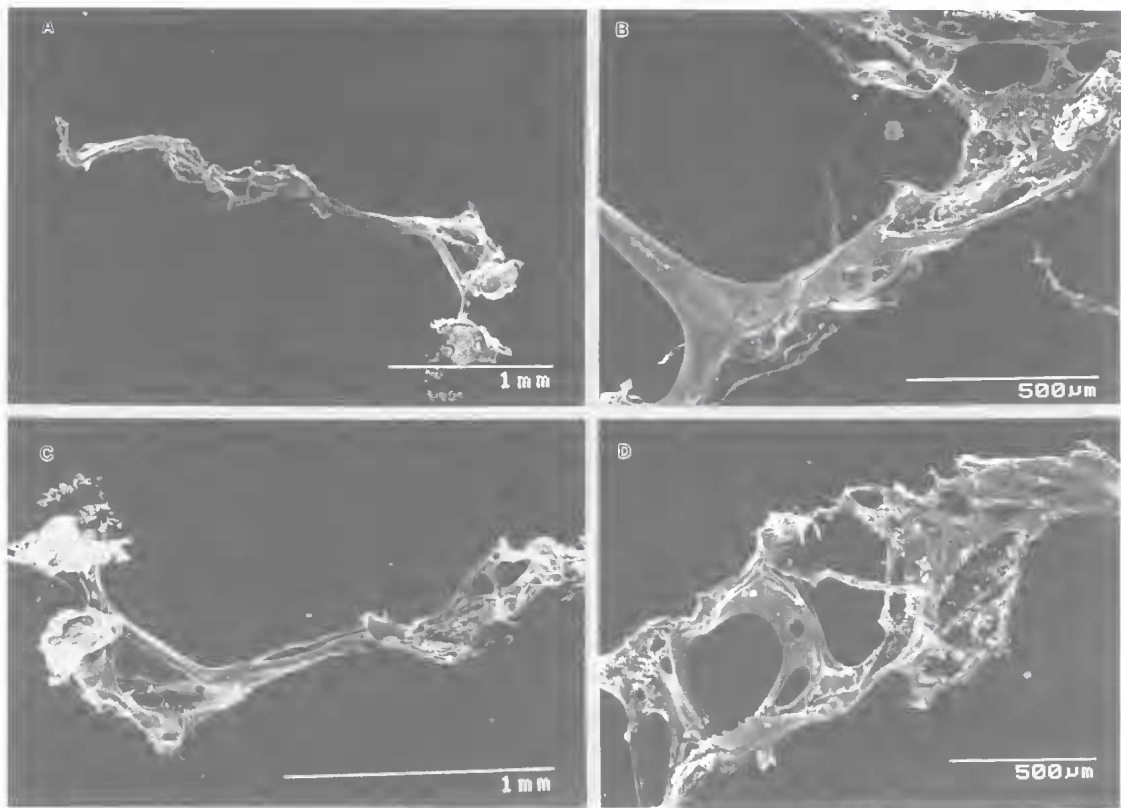


FIG. 2. *Aplysilla reticulata* sp. nov. A, Fasciculate fiber resulting from the fusion of two primary fibers, as shown by the presence of two basal plates. B, Detail of a primary fiber. C, Detail of the basal plates of a fasciculate primary fiber. D, Detail of secondary reticulation between two adjacent primary fibers. Fenestrated plates can also be seen.

because it lacks both the spongin spicules and the basal continuous plate of spongin that are characteristic of this genus (Bergquist, 1980). Moreover, *Igernella* species usually have massive habits and relatively large oscules, a much more regular and denser network of secondary fibers, and longer and less fasciculate primary fibers (e.g. Van Soest, 1978; Bergquist, 1980; Uriz & Maldonado, 1996).

Therefore, this new sponge combines the skeletal characteristics of the darwinellid genus *Pleraplysilla* and the dictyodendrillid genus *Igernella*, yet it cannot be assigned to either genera, unless the diagnosis of one of them is modified. On the one hand, if the acquisition of interconnecting secondary fibers is assumed to be a polyphyletic condition, the new sponge could be included in *Pleraplysilla* on the basis of its similarity in the structure of the primary fibers and the absence of spongin spicules. However, should this assumption be accepted, the

dictyodendrillid genus *Dictyodendrilla* Bergquist (with highly dendritic fibers anastomosed to form a network) and the darwinellid genus *Dendrilla* Lendenfeld (with highly dendritic fibers that do not anastomose) would have to be fused into a single taxonomic unit, since taxonomic separation is based solely on the skeletal pattern. The genera *Darwinella* and *Igernella* would remain distinct genera, not on the basis of different skeletons (dendritic versus reticulate), but on the presence of distinctive spongin spicules, which appear not to be homologous (Garrone, 1978; Bergquist, 1996). Spongin spicules have a concentric laminated structure in *Darwinella*, whereas they have helicoidal structure and incorporate deposits of lepidocrocite in *Igernella* (Garrone, 1978; Bergquist, 1996). Conversely, if the presence/absence of both spongin spicules and a basal plate of spongin is assumed not to be taxonomically relevant at the generic level, the new species

could also be assigned to *Igernella* on the basis of its reticulate skeleton. Again, to be consistent in the application of the taxonomic criterion, the genera *Darwinella* and *Aplysilla*, which are distinguished on the presence-absence of spongin spicules, would have to be fused into a single taxonomic unit.

This dilemma raises the same question that has troubled taxonomists for the past century: which set of skeletal features should be emphasised in Dendroceratida? Obviously, we do not have conclusive evidence to offer a definitive solution. Nevertheless, an analysis of available evidence suggests that certain assumptions on which the current classification of Dendroceratida is based need to be reassessed. It is a fact, for example, that reticulate skeletons display a wide variety of models of organisation not only within orders, but also families (e.g. Van Soest, 1978; Bergquist, 1980, 1995, 1996; Bergquist et al., 1998). Therefore, the acquisition of a reticulate skeleton is likely to have evolved independently in Dictyoceratida, Verongida and Dendroceratida. In this context, the hypothesis that interconnecting secondary fibers also evolved independently within Dendroceratida cannot be discarded. The taxonomic interpretation given for the pattern of chemical affinities (Bergquist et al., 1990) conflicts with that given for the histological findings (Vacelet et al., 1989; Boury-Esnault et al., 1990). However, it is noteworthy that both patterns of affinities agree in suggesting a relationship between the dictyodendrillid genus *Igernella* and some darwinellid genera, such as *Aplysilla*, *Darwinella*, *Pleraplysilla* and *Chelonaplysilla* de Laubenfels. In contrast, they do not support any relationship between *Igernella* and *Dictyodendrilla* (Bergquist et al., 1990), although both genera are currently allocated in the same family. Furthermore, evidence from both non-skeletal differences and skeletal differences are consistent in suggesting that *Igernella* and *Dictyodendrilla* may have acquired their reticulate skeleton through independent evolutionary pathways. In fact, as previously suggested by Topsent (1905), and further stated by Bergquist et al. (1990), "there is no real similarity between the fine, regular skeletal reticulum of *Dictyodendrilla* and the coarse, sparse and irregular pattern of *Igernella*".

This reanalysis of the available evidence, although still only offering a partial view of the evolutionary relationships, appears to support the hypothesis that the acquisition of a secondary

reticulate skeleton was probably a convergent process in Dendroceratida. This is of little surprise, since the anastomosis of skeletal elements (either spicules or ascending fibers), in the building of skeletal networks, is a condition that may have evolved independently many times in Porifera. Among other possibilities, the development of a skeletal network appears to be the result of selective pressure on thinly encrusting growth habits to increase body size. For example, several lines of encrusting axinellids and poecilosclerids share a similar, non-reticulate (typically hymedesmoid) skeletal architecture that has obviously evolved independently and that converges towards reticulate and plumo-reticulate patterns in massive and erect genera (e.g. Hooper, 1991, 1996). Similarly, Bergquist (1996) noted that most darwinellid sponges are encrusting, while the reticulate structure of the skeleton allows the Dictyodendrillidae to attain a large size. In this context, and by linking chemical, histological and skeletal data, it would be interesting to consider the possibility that some reticulate patterns, such as those of *Igernella*, may have evolved from skeletal models similar to those of *Pleraplysilla*, *Darwinella* and *Chelonaplysilla*. The genus *Dictyodendrilla*, however, appears to be chemically, cytologically, and skeletally unrelated to this set. Therefore, the possibility that the reticulate pattern of this genus, as well as that of the genus *Acanthodendrilla* Bergquist, may have evolved from a skeletal state similar to that of the genus *Dendrilla*, as fibers and morphology suggest, should be kept in mind. Indeed, some degree of fiber anastomosis has already been reported in species of both *Aplysilla* and *Dendrilla* by Van Soest (1987: *A. stocki*) and by Vacelet (1960: *D. cirsioides* Topsent), respectively.

In order to allocate our new species taxonomically, we have opted to expand the diagnosis of the genus *Pleraplysilla* to include species with an irregular network of secondary fibers, such as *Pleraplysilla reticulata* sp. nov. Nevertheless, this taxonomic allocation must be considered tentative, since the material studied was unsuitable for providing information on intra-specific skeletal variability, the diterpenoid chemistry, and choanocyte chamber structure. Such a taxonomic allocation comes into conflict with the current subdivision of Dendroceratida based on reticulate and dendritic skeletons. Although some preliminary ideas for a new classification have been put forward here, we

explicitly refuse to make any familial re-arrangement for several reasons: 1) the information available at present, though in conflict with the current taxonomic scheme, is still insufficient to support a robust alternative pattern of relationships at the family level; 2) re-arrangements at the suprageneric level must be based on re-examination of abundant type material, and fall beyond the scope of this study; and 3) the ideas proposed here can be discussed and reassessed in the context of the wide-ranging revision of the Dendroceratida that is being prepared, as announced by Bergquist et al (1998).

ACKNOWLEDGMENTS

We thank the technical staff of the Servicio de Microscopía de la Universidad de Barcelona for help in SEM study, Dr. R.W.M. van Soest (Zoölogisch Museum Amsterdam) for the loan of museum material, and members of the 'Fauna Ibérica - IV' cruise, especially J. Remón, for their willingness to help us in our ultimately fruitless attempt to collect additional material of this new species. This research was partially supported by funds of an EC grant (MAS3-CT97-0118).

LITERATURE CITED

- BERGQUIST, P.R. 1980. A revision of the supra-specific classification of the orders Dictyoceratida, Dendroceratida and Verongida (class Demospongiae). *New Zealand Journal of Zoology* 7: 443-503.
1995. Dictyoceratida, Dendroceratida and Verongida from the New Caledonia lagoon (Porifera: Demospongiae). *Memoirs of the Queensland Museum* 38(1): 1-51.
1996. Porifera: Demospongiae. Part 5. Dendroceratida and Halisarcida. *New Zealand Oceanographic Institute Memoir* 107: 1-53.
- BERGQUIST, P.R., KARUSO, P. & CAMBIE, R.C. 1990. Taxonomic relationships within the Dendroceratida: A biological and chemotaxonomic appraisal. Pp. 72-78. In Rützler, K. (ed.) *New Perspectives in Sponge Biology*. (Smithsonian Institution Press: Washington D.C.).
- BERGQUIST, P.R., WALSH, D. & GRAY, R.D. 1998. Relationships within and between orders of Demospongiae that lack a mineral skeleton. Pp. 31-40. In Watanabe, Y. & Fusetani, N. (eds) *Sponge sciences. Multidisciplinary perspective*. (Springer-Verlag: Tokyo).
- BOURY-ESNAULT, N., VOS, L. DE, DONADEY, C. & VACELET, J. 1990. Ultrastructure of choanosome and sponge classification. Pp. 237-244. In Rützler, K. (ed.) *New perspectives in sponge biology*. (Smithsonian Institution Press: Washington D.C.).
- DENDY, A. 1905. Report on the sponges collected by W. A. Herdman at Ceylon in 1902. Report to the Government of Ceylon on the Pearl Oyster Fisheries 3: 57-246.
- GARRONE, R. 1978. Phylogenesi of connective tissue. Morphological aspects and biosynthesis of sponge intercellular matrix. (S. Karger: Bâle).
- HOOPEY, J.N.A. 1991. Revision of the family Raspailiidae (Porifera: Demospongiae), with description of Australian species. *Invertebrate Taxonomy* 5: 1179-1418.
1996. Revision of Microcionidae (Porifera: Poecilosclerida: Demospongiae), with description of Australian species. *Memoirs of the Queensland Museum* 40: 1-626.
- SOEST, R.W.M. VAN 1978. Marine sponges from Curaçao and other Caribbean localities. Part 1. Keratosa. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 179: 1-94.
- TOPSENT, E. 1905. Etude sur les Dendroceratida. *Archives de Zoologie Expérimentale et Générale* (4) 3(8): 171-192.
- URIZ, M.J. & MALDONADO, M. 1996. The genus *Igernella* (Demospongiae: Dendroceratida) with description of a new species from the central Atlantic. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 66 (suppl.): 153-163.
- VACELET, J. 1960. Eponges de la Méditerranée nord-occidentale récoltées par le 'President Théodore Tissier' (1958). *Revue des Travaux de l'Institut des Pêches Maritimes* 24(2): 257-272.
- VACELET, J., BOURY-ESNAULT, N., VOS, L. DE & DONADEY, C. 1989. Comparative study of the choanosome of Porifera: II. The Keratose Sponges. *Journal of Morphology* 201: 119-129.